

# Some Taxonomic Revision in the Australian Marsupial Genus *Bettongia* (Macropodidae), with description of a New Species

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## 1. Introduction

This study was initiated by the problem of identifying cranial fragments of *Bettongia* found in cave deposits in the Buchan area of eastern Victoria. The name *B. gaimardi* was used (Wakefield, 1960) for the specimens concerned, but only out of consideration of the near-coastal habitat and the priority in the genus of this specific name.

Both Troughton (1941) and Tate (1948) knew *B. gaimardi* only as a "lost" species from central-eastern New South Wales, and each was vague or doubtful as to whether it was specifically distinct from *B. penicillata*. Finlayson (1958) treated *B. penicillata* as a species almost Australia-wide in distribution, but gave no cognizance to *B. gaimardi*.

The present investigation was broadened to a study of morphological characters and geographical distribution of all species of the genus. Specimens were examined from the following sources:

National Museum of Victoria, Melbourne (NMV)  
Fisheries and Wildlife Department, Melbourne  
Australian Museum, Sydney (AM)  
Macleay Museum, Sydney  
Queensland Museum, Brisbane  
South Australian Museum, Adelaide  
Western Australian Museum, Perth  
Tasmanian Museum, Hobart  
Queen Victoria Museum, Launceston

American Museum of Natural History, New York (AMNH)  
Museum of Comparative Zoology, Harvard University (MCZ)

In addition, data of specimens, including photographs and measurements, were obtained from:

British Museum (Natural History), London (BM)  
National Museum of Natural History, Paris  
Zoological Museum, Oslo University, Norway

Of the now-extinct mainland population of *B. gaimardi*, all sources together yielded only 7 adult skulls complete enough for suitable measurement. A series of 11 skulls of the extant Tasmanian population (syn. *B. cuniculus*) has been used to compare this island race with the *B. gaimardi* of the mainland; and the combined series of 18 specimens has provided data for comparisons with other species.

A series of 14 adult skulls of the extant south-western Australian population has been used to demonstrate characters of *B. penicillata*. Of the hitherto undescribed species in north-eastern Queensland, only 6 specimens were located (4 adults and 2 sub-adult); these however amply demonstrate a species of brush-tailed bettong distinct from both *B. penicillata* and *B. gaimardi*.

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## 2. The genus *Bettongia*

In this study, the fourth species, *B. lesueur*, has been considered only sufficiently to distinguish it in general terms from the three brush-tailed species with which the present paper is primarily concerned.

Terms used for cranial measurements are either as standardized by Thomas (1888, p. viii), or are self-explanatory, or are as follows:

**Rostrum Width.** The maximum width at junction of maxillae and premaxillae.

**Nasal Opening Width.** The maximum internal width at the posterior end of nasal passage.

$p^4-p^4$  and  $m^4-m^4$ . The maximum distance, in each case, between outer edges of these teeth.

**Bulla Length.** From the anterior edge of the foramen lacerum posterio- rum to the anteriormost part of the alisphenoid inflation.

**Bulla Depth.** The maximum vertical depth of the alisphenoid inflation below the horizontal condyloid surface of the glenoid fossa.

Unless otherwise indicated, measurements throughout the paper are in millimetres.

Range and mean of each measurement for each population are set out in Table 1.

The series have been compared for skull size on the basis of one measurement only—Basal Length. The more important consideration of cranial proportions has been based on the reduction of other dimensions to percentages of Basal Length; these proportions are summarized in Table 2.

Because of the smallness of the samples used in the comparisons, statistical significance has been assessed by the Mann-Whitney *U* test, as described by Siegel (1954).

Distributional data are shown in Text-figure 1.

The genus was established by Gray (1837). Its species are distinguished by the combination of three "ill-defined characters" (Tate, *loc. cit.*): large palatal vacuities, inflated bullae, and the permanent premolar having 6 or more vertical grooves. There are four species.

*Bettongia lesueur* inhabits comparatively arid areas, living in warrens which it digs in sandy soil. Its fur is soft and woolly, and the dorsal hair of the tail is short (about 1 cm long). In these features of home and pelage, it is distinct from all other species of the genus.

In the other three species, the general pelage is of comparatively coarse hair, and the apical quarter to half of the tail carries a dorsal crest of long dark hair (to about 2 cm. long). Two of these species, and presumably the third, gather grass and similar materials, which they carry in the prehensile tail, to construct nests for daytime shelter. They are collectively referred to as the "brush-tailed bettongs" or "nest-building bettongs".

In cranial characters, *B. lesueur* is distinguished from the other species by (a) the proportionately shorter, "pinched-in" rostrum; (b) the major inflation of the auditory bullae (Bulla Length about 25 per cent, and Bulla Depth about 23 per cent, of Basal Length); (c) the large size of the premolars ( $p^4$  length is about 14 per cent of Basal Length); and (d) the steep size gradient of the molars, with the  $m^4$  very small.

All these cranial features appear to be specializations which contrast with a comparatively unspecialized state in *B. gaimardi* (rostrum long and broad, bullae not much inflated, premolars comparatively small, and molar gradient slight). Tate (*loc. cit.*) had similar thoughts in considering *B. cuni-*

*culus* (= *B. gaimardi*) to be the "most primitive of living *Bettongia*". Intermediate degrees of specialization are seen in the other two species of the genus.

### 3. *Bettongia penicillata*

Originally described by Gray (*loc. cit.*), the type specimen, from "New South Wales", is in the BM (No. 50.11.22.47; skull, 279f; skin, 298c). Of the skull, J. E. Hill states (*in litt.*, 4.7.1963): "pm<sup>4</sup> with strongly sloping external lateral alveolar rim, much lower posteriorly: axis of pm<sup>4</sup> flexed outward anteriorly: toothrows divergent (m<sup>4</sup>-m<sup>4</sup> 16.7; pm<sup>4</sup>-pm<sup>4</sup> 21.1)".

In lower as well as upper premolars, while the serrated sectorial edge of the tooth is approximately horizontal, the edge of the enamel adjacent to the alveolus is parallel to the alveolar rim. Consequently, the anterior edge of the grooved enamel is vertically about twice as long as the posterior edge. This shape, and the outward flexing of the premolars, are diagnostic of *B. penicillata* and distinguish it absolutely from the three other species of the genus\*. (See Plate 1.)

The auditory bullae of *B. penicillata* are large, the tooth-rows converge posteriorly, and the fourth molars are small. (See Table 1.)

Normally, all the hair of the caudal crest, including the terminal tuft, is dark brown or black, but two exceptions are known: Waterhouse (1846) cites a specimen with a white terminal tail-tuft, and NMV No. 21764 from near Mildura has a similarly white-tipped tail.

There is a paucity of locality data for the eastern Australian population of *B. penicillata*. Thomas (*loc. cit.*) cited 3 New South Wales specimens

(the type, and two from "Liverpool Plains" and "Namoi River" respectively) and 6 from South Australia (including two from "scrub near Adelaide", and the type of *Bettongia gouldii* (Waterhouse, 1846) from the head of St. Vincent Gulf).

Two other New South Wales specimens, AM Nos. A16792 and M1835, cited by Marlow (1958) as *B. penicillata*, are, in fact, *B. lesueur* and *B. gaimardi* respectively.

Kreff (1866) found the species abundant in 1857 about the Murray River from Euston (N.S.W.) westward. Apparently the nominate race, *B. penicillata penicillata*, extended from north-eastern New South Wales to the St. Vincent Gulf area of South Australia. In the present study, no assessment is made of either cranial or plastic characters of this form.

Waterhouse (1841) described a specimen from Swan River, Western Australia, as *Hypsiprymnus ogilbyi*. Examples (of *B. penicillata*) from south-western Australia were said to be "generally somewhat darker in the colouring of the feet and tail than those from New South Wales" (Waterhouse, 1846). In the Western Australian Museum there is a series of 18 skins, all from south of latitude 32°S and west of longitude 120°E, comprising about equal numbers of dark brown, medium brown and light brown specimens. The south-western Australian population is currently accorded subspecific status as *B. penicillata ogilbyi*. Thomas (*loc. cit.*) cited one BM specimen from "Shark's Bay, W.A."

South Australian Museum No. M4140 is a skin-skull specimen of a very juvenile *B. penicillata* collected near Waldana Spring, about 125 miles north-west of Ooldea, South Australia. Finlayson (1958) gave details of reports which indicated a population of the species from the Ooldea area northwards to the Musgrave Range region

\* In the Macropodidae the morphology of the permanent premolar appears to be more important in taxonomy than any of the other characters dealt with in this paper.

about the Northern Territory border. This suggests that there was a continuous distribution of *B. penicillata* from south-western to south-eastern Australia, in which case the validity of the present subspecific classification within the species (see Iredale and Troughton, 1934) is doubtful.

Finlayson (1957) described *Bettongia penicillata anhydra* from central-western Northern Territory (22°2'S, 129°47'E). The type specimen (South Australian Museum No. M3582) comprises a skull only, with much of its posterior part missing (see Plate 1). In this specimen, several features (short rostrum, very large bullae, and proportionately long premolars) demonstrate that it belongs not to *B. penicillata* but to *B. lesueur*\*.

Besides the deletion of the area of "anhydra", the distribution of *B. penicillata*, as shown by Finlayson (1958, fig. 2), must be reduced by at least the following areas:

(a) North-eastern Queensland, (b) Eastern Queensland (Dawson Valley), (c) South-eastern Queensland (Pine Mountain), and (d) Western Victoria (Grampians). Of these, (a) and (b) apply to the hitherto undescribed species (see Section 5), while (c) and (d) apply to *B. gaimardi* (see Section 4b).

#### 4. *Bettongia gaimardi*

##### a. *Typification*:

The species was originally described by Desmarest (1822), as *Kangurus gaimardi*. It was based on a specimen (Paris Museum No. 79a), collected in 1819 during the voyage of the *Uranie*, and of which the author stated, "M. Gaimard l'a trouvé aux environs

de port Jackson". The same specimen was also named *Kangurus lepturus* (Gaimard, 1824) and *Hypsiprymnus white* (Quoy and Gaimard, 1824).

Associated with this last description, drawings of animal and skull were published. The illustration of the animal cannot be regarded as accurate, for it has abnormally large ears and the tail is shown without the crest of long hairs.

Desmarest (*loc. cit.*) described the tail as "gris-roussâtre devenant plus foncé et passant au brun dans le bout", while Quoy and Gaimard (*loc. cit.*) said "son extrémité est terminée par un bouquet de poils". J. Dorst states (*in litt.*, 4.7.1963) that "the type of the species is in very poor condition, especially the tail is badly damaged and the hairs are worn out. It does not show any crest [but] there is a very faint indication that perhaps there was one; there is no indication of a white apex".

The illustration by Quoy and Gaimard of the type skull is reproduced in Plate 1. It shows the grooved surfaces of the premolars to be long horizontally and shallow vertically, though the outer alveolar rim of the p<sup>4</sup> is shown with more slope than is normal in the species.

Associated at present with the type skin is a skull (Paris Museum No. A2650) of *B. penicillata* (see Plate 1). The incomplete state of this specimen and the features of its premolars show that it is not the type skull illustrated by Quoy and Gaimard. It has the appearance of a skull picked up in the field after having been damaged by scavengers. Apparently the type skull is now lost.

Fortunately, Waterhouse (1846) recorded descriptions of both pelage and skull of the type specimen of *B. gaimardi*. He described the tail as "of a brightish rust colour above, paler

\* The skull is very small (Zygomatic Width 37.1, m<sup>1-3</sup> 10.5) but with Bulla Depth 11.7 and p<sup>4</sup> Length 7.6. The proportions Bulla Depth/Zygomatic Width (31 per cent) and p<sup>4</sup> Length/m<sup>1-3</sup> Length (72 per cent) are those of *B. lesueur* and exceed maximum values for corresponding proportions in each of the other three species.



beneath, the apical third clothed on the upper surface with longish, bushy, brown-black hairs, but at the extreme point with a few white hairs”.

Waterhouse's measurements (converted to metric scale) for the type skull are:

Total length of cranium, 74.1  
Zygomatic Width, 42.3  
Nasals Length, 30.7  
Nasals, greatest width, 14.4  
Nasals, width at anterior end of premaxillae, 6.3  
Interorbital Width, 19.8  
p<sup>1</sup> Length, 7.9

Troughton (*loc. cit.*) stated:

The animal was said to have been taken in the interior of the “Montagnes-bleues de la Nouvelle-Hollande”, referring to the eastern slopes of the range west of Sydney.

This is a misinterpretation of the following notes which Quoy and Gaimard (*loc. cit.*) appended to their description of *Hypsiprymnus white*:

Dans un voyage que nous fîmes dans l'intérieur des Montagnes-bleues de la Nouvelle-Hollande, nous eûmes occasion d'en voir un . . . Nous croyons que c'est une variété de l'espèce que nous venons décrire.

Actually, the two Frenchmen went inland as far as Bathurst, on the road constructed in 1815 across the Blue Mountains. There is apparently no record in the literature as to how and precisely where Gaimard obtained the original specimen of *B. gaimardi*.

#### b. Mainland Distribution:

The BM has three specimens, two from “New South Wales” and a third without record of locality.

[One of the former, No. 41.1140, was reported by R. E. Hill (*in litt.*, 25.5.1963) to have originated from “Liverpool Plains”, but later (*in litt.*, 6.7.1966), he expressed doubt on the point and remarked that Thomas (*loc. cit.*) had noted no such locality for it.]

In the AM there are three specimens:

No. 1121. Pine Mountain, south-eastern Queensland. A juvenile skull. (Collected about 1869.) (This specimen is identified as *B. gaimardi* because of the morphology and size of the p<sup>3</sup>, the grooved enamel of which is 2.4 mm. in vertical depth at both anterior and posterior ends, as compared with about 4 mm. and 2 mm. respectively for these measurements in *B. penicillata*.)

No. S583. Campbelltown. An adult skeleton. (Registered in 1896.)

No. M1835. Balmoral. A subadult skin and skull. (Registered in 1906.)

In the Macleay Museum there are an adult skull and a subadult skull, neither with locality data. Presumably they are from eastern New South Wales. Their cranial and dental dimensions are of the small mainland race, not the large Tasmanian form.

In the NMV there are 7 specimens:

No. C2448. Upper Yarra. A mounted skin. (Registered in 1877.)

No. C2450. “Melbourne”. A mounted skin. (Received in 1867.)

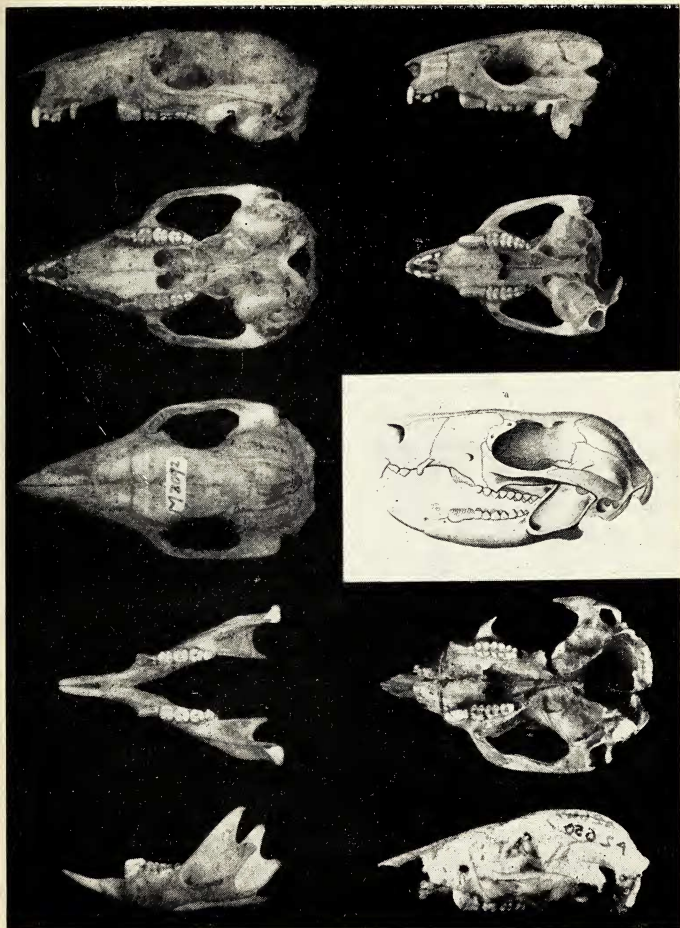
No. C6865. “Melbourne”. A subadult skeleton. (Received in 1869.)

No. C6866. Goulburn River. A subadult skull. (Received in 1861.)

Nos. C6867, C6868, C6869. “Victoria”. Adult skulls. Re-registered in 1902, from “old collection”.

The one-time distribution of *B. gaimardi* in western and south-western Victoria is evidenced by the occurrence of skeletal remains in caves at Mount Hamilton, the Grampians, and near Portland (Wakefield, 1963a, 1963b, 1963c). One sub-fossil cranium (NMV No. P20674), from Fern Cave near Portland, is obviously of modern age.

Finlayson (1958) stated that he had “accounts of a nest building betong from West Victoria generally in 1854, and the Grampians district in



Cranial Details of *Bettongia*.

Left side: Specimen of *Bettongia penicillata ogilbyi* (AM No. M3092).

Right side: { Upper—Type specimen of *Bettongia penicillata anhydra* (S. Aust. Mus. No. M3582).  
 { Middle—Illustration by Quoy and Gaimard of type skull of *Bettongia gaimardi*.  
 { Lower—Specimen A2650, Mus. Nat. Hist. Paris (lower illustration is mirror image of right side of skull).

1910", and he assumed that these applied to *B. penicillata*. However, they are far more likely to have referred to *B. gaimardi*, as there is no valid record, sub-fossil or otherwise, of *B. penicillata* in any part of Victoria except the extreme north-west (ref., Wakefield, 1966).

Finlayson (1959), in identifying fossil specimens from Tantanoola (far south-eastern South Australia) as "a somewhat microdont phase of *B. cuniculus*", unwittingly made a nice identification of *B. gaimardi* and foreshadowed the taxonomic conclusion which is reached in the next subsection of the present paper. Brazenor (1950) had already listed *B. cuniculus* as a one-time Victorian species but without indication of the basis of the record.

The mainland population, presumably now extinct, occurred as a modern animal about the Eastern Highlands and adjacent coastal tracts of south-eastern Australia, from south-eastern Queensland to south-western Victoria. It should be classified as the nominate subspecies with the trinomial *B. gaimardi gaimardi*.

#### c. Further Taxonomy:

Ogilby (1838) described a specimen, which he cited as from "Hunter's River, New South Wales", as *Hypsiprymnus cuniculus*, and he gave data of external features only.

Waterhouse (1846) suggested that an error of locality had been made in this case and that the specimen actually originated in Tasmania. He cited measurements of the type skull which, converted to metric scale, included: Nasals Length 35, Nasals Greatest Width 17,  $p^4$  Length 8.2. Thomas (*loc. cit.*) reported further data of the teeth:  $M^{1-3}$  13.8,  $m^4$  Length 4.0. All these measurements suggest a Tasmanian specimen (see Table 1).

The Tasmanian animal is given

specific status in current literature (Iredale and Troughton, *loc. cit.*; *et al.*) as *Bettongia cuniculus*. However, its dentition and, with one exception, its cranial proportions, are not significantly different from those of the mainland *B. gaimardi*.

In linear dimensions, as indicated by Basal Length of skull, the Tasmanian animal averages about 10 per cent larger than the mainland form. (For this comparison,  $p < 0.002$ .)

In proportion to Basal Length, the auditory bullae are significantly longer in the mainland form than in the Tasmanian. (In the comparisons of Bulla Length/Basal Length,  $p < 0.02$ .)

Referring to the type specimen and two others in the BM, J. E. Hill observed (*in litt.*, 3.4.1963): "The type specimen agrees well with the other two specimens and has a tail crest of short, dark brown hairs extending only for the terminal quarter of the length of the tail. Specimens referred to *B. gaimardi* have a tail crest of longer, blackish hairs, extending over the terminal half of the length of the tail."

The larger size, the proportionately less developed bullae, and the less developed caudal crest, are sufficient for the island population to be given subspecific status, with the trinomial *B. gaimardi cuniculus*.

#### d. General Characters:

The dorsal body colour of *B. gaimardi* is light brown ticked whitish, merging to whitish beneath. This is apparently a uniform character, in contrast to the individual variation noted in *B. penicillata*. The pelage of *B. gaimardi* is about the same as that of the lighter variants of *B. penicillata*.

Typically, the long dark hairs of the caudal crest give way to a white tuft which comprises the apical  $\frac{1}{2}$  to  $1\frac{1}{2}$  inches of the tail hair.\* An exception

\* In several museum specimens, the apical part of the tail and the white tuft has been lost due to careless skinning.

is provided by a single Tasmanian skin which had only "a few silver-grey hairs in the tail tip" (R. H. Green, *in litt.*, 22.5.1963).

In summary: The white tail-tip is almost invariably present in both population of *B. gaimardi* but is almost invariably absent in *B. penicillata*.

In Tables 1 and 2 there are data of 7 specimens of *B. gaimardi gaimardi*: BM No. 55.12.26.199; AM No. S583; NMV Nos. R2177, R2178, R2179, P20674; Macleay Museum No. M1166.

Besides the differences of shape and insertion of the  $p^4$ , the cranial proportions that distinguish *B. gaimardi* from *B. penicillata* are:

(a) Interorbital region less constricted (Interorbital Width greater).

(b) Rostrum less tapered (Nasal opening wider).

(c) Bullae less inflated (Length and Depth each less).

(d) Larger molars ( $m^{1-3}$  Length and  $m^4$  Length each greater).

(e) Tooth-rows closer to parallel ( $p^4-p^4$  Width less,  $m^4-m^4$  Width greater).

In all eight relevant comparisons, the differences between the two species are highly significant ( $p < 0.002$  in each case).

## 5. *Bettongia tropica* sp. nov.

### a. *Diagnosis*:

*Bettongia*; similar in size, pelage and caudal crest to both *B. gaimardi* and *B. penicillata*; similar in cranial proportions to *B. penicillata*; interorbital width less, rostrum narrower, bullae much larger, than in *B. gaimardi*; permanent premolars inserted and shaped as in *B. gaimardi* but longer, neither anteriorly flexed outward nor with anterior edge vertically long as in *B. penicillata*; molars similar to those of *B. gaimardi* but the

fourth smaller, all larger than in *B. penicillata*.

### b. *Type Specimen*:

NMV No. C6870 (ex MCZ No. 29207). Adult male, skin and skull. Mount Spurgeon, 3700 feet, north-eastern Queensland. Collected July 24, 1932, by P. J. Darlington. Plate 3, left side.

Total Length 657; Tail 320; Pes 124; Ear 38; Claws of Manus (in order) 7, 11, 13, 11.5, 7; Claw of 4th Digit of Pes 17.

General dorsal coloration brown ticked whitish; individual hairs bluish-grey at base, subterminal zone pale grey, terminally rich brown; guard hairs silver. Crown and face dark brown, about ears fawn, ears medium brown. Sides pale brown; underparts, from throat to belly, pale bluish-grey. Beneath tail with long appressed hair, rufous for first few centimetres then silvery; above tail similar to body for first few centimetres, then silver guard hairs gradually replaced by dark hairs which eventually form the dorsal brush of dark brown to black hair reaching maximum length (about 20 mm.) on terminal 10 cm. of tail; no whitish tail tip. Front limbs with long hair, which is especially noticeable (about 10 mm. long) on manus and digits. Hind limbs with short appressed hair which becomes long (about 10 mm.) on 4th digit; feet dull pale brown.

Cranial Dimensions: Basal Length 65.5; Zygomatic Width 41.8; Interorbital Width 16.6 approx.; Nasals Length 28.9; Nasals, Greatest Width 13.2; Rostrum Width 13.8; Nasal Opening Width 7.5;  $p^4-p^4$  19.4;  $m^4-m^4$  17.0; Palatal Length 42.5; Anterior Palatal Foramen Length 2.9; Bulla Length 14.2; Bulla Depth 10.8, 11.0;  $p^4$  Length 8.4;  $m^{1-3}$  Length 12.6;  $m^4$  Length 3.0, Width 2.8.

TABLE 1

Cranial measurements of Species of *Bettongia* (in millimetres).

In each case the upper figures give the Range and the lower figure, in parenthesis, is the Mean.

|                                      | <i>B. gainardi</i><br>7 specimens | <i>B. gainardi cuniculus</i><br>11 specimens | <i>B. penicillata ogilbyi</i><br>14 specimens | <i>B. tropica</i><br>4 specimens |
|--------------------------------------|-----------------------------------|--|---|----------------------------------|
| Basal Length                         | 63.2-67.5<br>(64.4)               | 67.8-73.3<br>(70.6)                          | 61.1-73.0<br>(66.5)                           | 63.4-65.5<br>(64.2)              |
| Zygomatic Width                      | 40.3-43.4<br>(42.2)               | 42.4-46.5<br>(45.3)                          | 38.5-45.8<br>(42.2)                           | 40.1-41.8<br>(41.2)              |
| Interorbital Width                   | 17.2-20.0<br>(18.5)               | 18.1-21.0<br>(19.9)                          | 15.9-18.8<br>(17.4)                           | 13.5-18.0<br>(15.8)              |
| Nasals Length                        | 29.9-31.7<br>(30.8)               | 33.3-36.2<br>(34.7)                          | 28.6-36.5<br>(32.5)                           | 27.6-32.5<br>(29.6)              |
| Nasals, Greatest Width               | 12.3-15.8<br>(13.9)               | 12.0-16.0<br>(14.5)                          | 11.1-15.5<br>(13.5)                           | 13.1-14.3<br>(13.5)              |
| Rostrum Width                        | 14.6-16.0<br>(15.4)               | 16.0-18.6<br>(17.4)                          | 13.7-17.6<br>(16.0)                           | 13.7-15.0<br>(14.3)              |
| Nasal Opening Width                  | 7.9-9.5<br>(8.7)                  | 8.6-9.8<br>(9.1)                             | 7.0-9.3<br>(7.9)                              | 7.3-8.3<br>(7.8)                 |
| Bulla Length                         | 11.7-12.6<br>(12.1)               | 11.7-13.0<br>(12.5)                          | 12.4-15.6<br>(14.2)                           | 13.4-14.2<br>(13.8)              |
| Bulla Depth                          | 8.4-9.9<br>(9.1)                  | 8.7-10.3<br>(9.5)                            | 9.2-11.6<br>(10.6)                            | 10.6-11.0<br>(10.9)              |
| P <sup>1</sup> -P <sup>4</sup> Width | 18.9-20.5<br>(19.7)               | 20.5-23.3<br>(21.7)                          | 19.0-23.5<br>(21.5)                           | 19.4-20.9<br>(20.0)              |
| M <sup>1</sup> -M <sup>4</sup> Width | 17.9-19.9<br>(18.8)               | 19.1-21.6<br>(20.4)                          | 15.0-18.8<br>(16.8)                           | 16.4-18.3<br>(17.2)              |
| P <sup>4</sup> Length                | 6.7-7.5<br>(7.2)                  | 7.7-8.9<br>(8.1)                             | 6.5-7.6<br>(7.3)                              | 7.8-8.6<br>(8.3)                 |
| M <sup>1-3</sup> Length              | 12.0-13.4<br>(12.8)               | 13.0-14.2<br>(13.7)                          | 11.4-13.8<br>(12.4)                           | 12.6-13.6<br>(13.2)              |
| M <sup>4</sup> Length                | 2.9-3.8<br>(3.3)                  | 3.2-4.4<br>(3.8)                             | 2.2-3.0<br>(2.6)                              | 2.6-3.0<br>(2.8)                 |

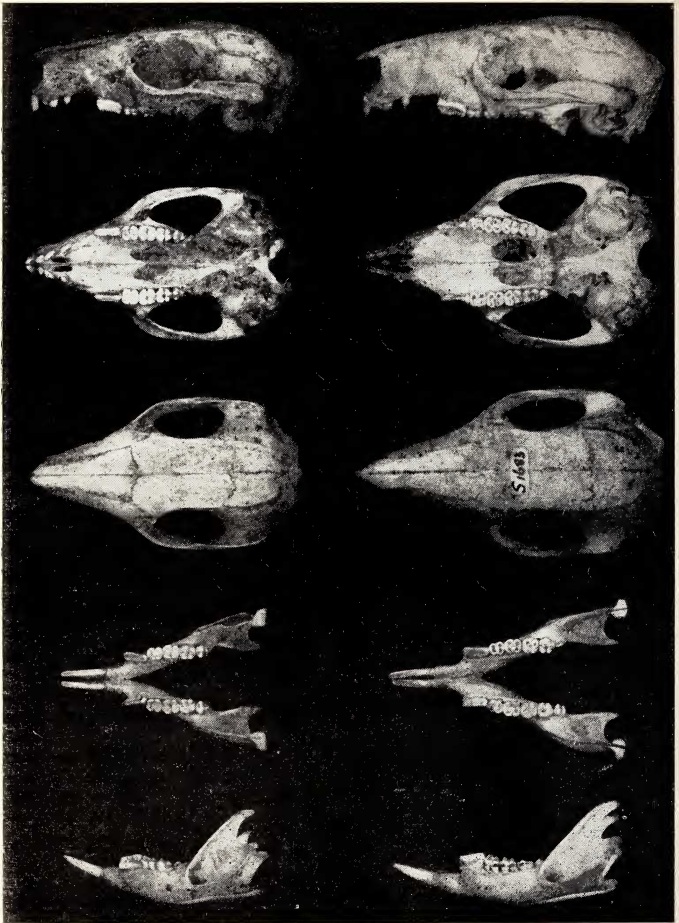
TABLE 2

Cranial proportions of species of *Bettongia* (percentages of Basal Length).

In each case the upper figures give the Range and the lower figure, in parenthesis, is the Mean.

|  | <i>B. gaimardi gaimardi</i><br>7 specimens | <i>B. gaimardi cuniculus</i><br>11 specimens | <i>B. gaimardi</i> : Data of<br>two races combined<br>18 specimens | <i>B. penicillata ogilbyi</i><br>14 specimens | <i>B. tropica</i><br>4 specimens |
|--|--|--|--|---|----------------------------------|
| <u>Zygomatic Width</u>                   | 63.8-68.4                                  | 61.4-65.1                                    | 61.4-68.4  | 60.0-67.2                                     | 63.3-65.2                        |
| B.L.                                     | (66.9)                                     | (63.9)                                       | (64.8)   | (63.4)  | (64.1)                           |
| <u>Interorbital Width</u>                | 27.4-31.5                                  | 26.2-30.1                                    | 26.2-31.5  | 23.7-28.6                                     | 20.9-28.3                        |
| B.L.                                     | (28.8)                                     | (28.7)                                       | (28.7)   | (26.2)  | (24.6)                           |
| <u>Nasals Length</u>                     | 47.0-48.9                                  | 47.5-50.6                                    | 47.0-50.6  | 45.8-52.6                                     | 43.1-51.1                        |
| B.L.                                     | (47.9)                                     | (48.9)                                       | (48.5)   | (48.4)  | (46.3)                           |
| <u>Nasals, Greatest Width</u>            | 18.4-24.9                                  | 17.4-23.1                                    | 17.4-24.9  | 17.9-22.8                                     | 20.2-22.5                        |
| B.L.                                     | (21.9)                                     | (22.6)                                       | (22.3)   | (20.9)  | (21.1)                           |
| <u>Rostrum Width</u>                     | 21.6-25.2                                  | 22.7-25.9                                    | 21.6-25.9  | 22.4-25.4                                     | 21.1-23.4                        |
| B.L.                                     | (23.8)                                     | (24.6)                                       | (24.3)   | (23.9)  | (22.3)                           |
| <u>Nasal Opening Width</u>               | 12.4-15.0                                  | 12.1-14.4                                    | 12.1-15.0  | 10.7-14.0                                     | 11.4-13.0                        |
| B.L.                                     | (13.6)                                     | (12.9)                                       | (13.2)   | (11.9)  | (12.1)                           |
| <u>Bulla Length</u>                      | 17.8-19.7                                  | 17.0-18.7                                    | 17.0-19.7  | 20.3-21.9                                     | 21.1-21.7                        |
| B.L.                                     | (18.7)                                     | (17.7)                                       | (18.2)   | (21.3)  | (21.5)                           |
| <u>Bulla Depth</u>                       | 13.2-15.6                                  | 12.5-14.8                                    | 12.5-15.6  | 14.3-17.2                                     | 16.7-17.3                        |
| B.L.                                     | (14.2)                                     | (13.5)                                       | (13.8)   | (16.1)  | (17.0)                           |
| <u>P<sup>4</sup>-P<sup>4</sup> Width</u> | 28.9-32.2                                  | 28.7-31.8                                    | 28.7-32.2  | 31.1-36.1                                     | 29.6-32.9                        |
| B.L.                                     | (30.7)                                     | (30.7)                                       | (30.7)   | (32.3)  | (31.2)                           |
| <u>M<sup>4</sup>-M<sup>4</sup> Width</u> | 27.7-31.3                                  | 27.1-30.3                                    | 27.1-31.3  | 24.4-26.5                                     | 25.4-28.9                        |
| B.L.                                     | (29.4)                                     | (28.8)                                       | (29.0)   | (25.1)  | (27.2)                           |
| <u>P<sup>4</sup> Length</u>              | 10.6-11.9                                  | 11.0-12.1                                    | 10.6-12.1  | 10.0-11.8                                     | 12.1-13.6                        |
| B.L.                                     | (11.2)                                     | (11.5)                                       | (11.4)   | (10.7)  | (12.9)                           |
| <u>M<sup>1-3</sup> Length</u>            | 18.1-20.9                                  | 18.4-20.7                                    | 18.1-20.9  | 17.0-19.6                                     | 19.2-20.9                        |
| B.L.                                     | (19.8)                                     | (19.2)                                       | (19.5)   | (18.4)  | (20.5)                           |
| <u>M<sup>4</sup> Length</u>              | 4.6-5.6                                    | 4.5-6.3                                      | 4.5-6.3  | 3.4-4.2                                       | 4.1-4.7                          |
| B.L.                                     | (5.1)                                      | (5.4)  | (5.3)  | (3.9)   | (4.4)                            |

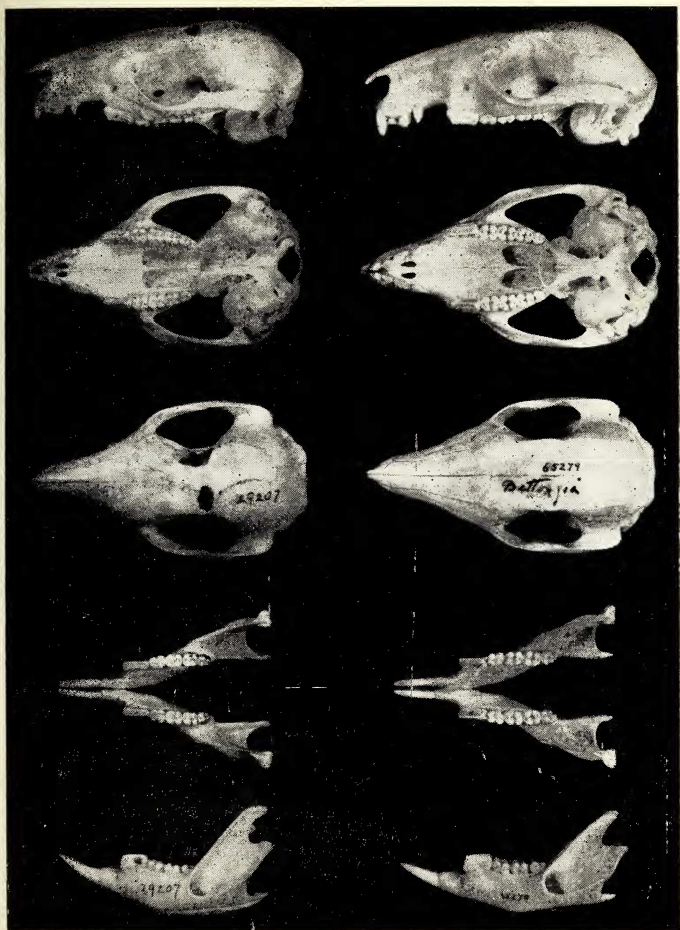




Cranial Details of *Bettongia gaimardi*.

Left side: Specimen of *B. gaimardi gaimardi* (Macleay Museum No. M1166).

Right side: Specimen of *B. gaimardi cuniculus* (AM No. S1683).



Cranial Details of *Bettongia tropica*.

Left side: Type specimen (NMV No. C6870). Right side: Specimen AMNH No. 65279.

[Figures in Plates 1, 2 and 3 are approximately two-thirds actual size.]

c. *Other Specimens:*

Darlington collected two other specimens, also at Mount Spurgeon, in July 1932:

MCZ No. 29205, adult female, slightly more brown than type. Total Length 641, Tail 335, Pes 123, Ear 40. Claws of Manus 5, 9, 14.5, 13, 5. Claw of 4th Digit of Pes 14.

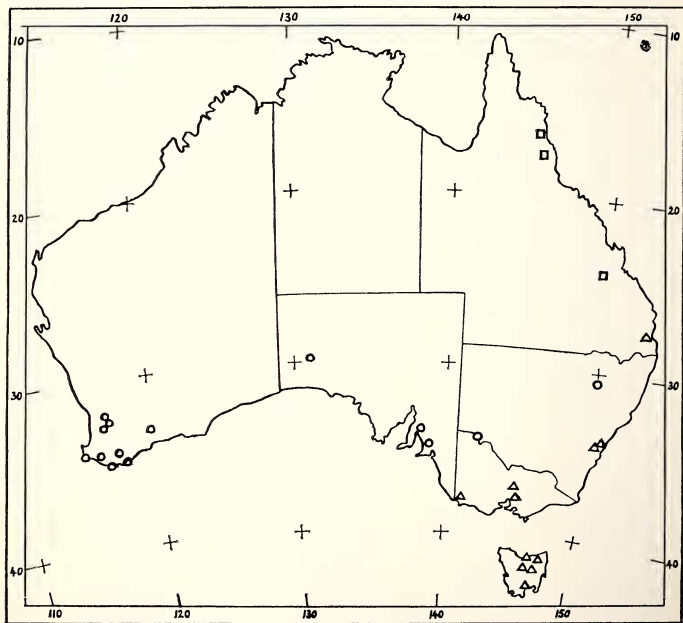
MCZ No. 29206, subadult male, general coloration much paler than in the two adults and tail with terminal tuft of silvery hair. Total Length

631, Tail 329, Pes 116, Ear 36. Claws of Manus 6, 10, 13.5, 13, 4.

In May 1922, H. C. Raven acquired two specimens from Vine Creek, Ravenshoe, north-eastern Queensland. AMNH Nos. 65279 (adult) and 65280 (subadult), but only skulls were preserved. (See Plate 3, right side.)

The sixth specimen, comprising a skin and skull, is located in the Zoological Museum of the Oslo University, Norway. Of it, E. K. Barth stated (*in litt.*, 25.11.1963), "On the tail it has a marked dorsal crest with maximum

TEXT-FIGURE 1



Localities of Specimens of *Bettongia*.

○ — *B. penicillata*    △ — *B. gaimardi*    □ — *B. tropica*

hair length 22 mm." and "the apical hairs of the tail are the same colour as the whole tail crest". The specimen was collected by Lumholtz in January 1884 at Coomboolaroo, Dawson Valley, eastern Queensland.

The identification of the south-eastern Queensland specimen (AM No. 1121) as *B. gaimardi* and not *B. tropica* is based on the small size and the few grooves of the deciduous third premolar ( $p^3$  Length 4.5, grooves 4 only). (See Section 4b.)

*d. Cranial Characters:*

In size and proportions, the skull is almost the same as that of *B. penicillata*, the Interorbital Width being less than in *B. gaimardi*. The rostrum is narrower than in either *B. gaimardi* or *B. penicillata*. The auditory bullae are proportionately much larger than those of *B. gaimardi*, slightly larger than those of *B. penicillata*, and not as large as those of *B. lesueur*. In disposition and size gradient, the molars are similar to those of *B. gaimardi* except that the fourth is smaller, and they are all proportionately larger than in *B. penicillata*.

As in *B. lesueur* and *B. gaimardi*, the permanent premolars ( $p_1$ ,  $p^4$ ) are long, and they are not flexed outward anteriorly. In proportion to skull size, the premolar length is less than that of *B. lesueur* and greater than that of *B. gaimardi*. The vertical grooves number 8-9, compared with 7-8 (or less) in *B. gaimardi*.

In the two subadult specimens of *B. tropica*, the deciduous third premolar ( $p^3$ ) has 6 grooves, as compared with 5 (rarely 4) in *B. gaimardi*. The length of  $p^3$  in both these specimens of *B. tropica* is 5.5, compared with averages of 4.8 and 5.3 for *B. gaimardi gaimardi* and *B. g. cuniculus* respectively.

Data of measurements of cranial and dental characters of *B. tropica*

are set out in Table 1 and proportions are set out in Table 2. The data are of 4 specimens: NMV No. C6870, MCZ No. 29205, AMNH No. 65279, and the Oslo skull.

In comparisons between *B. tropica* and *B. penicillata*, the following orders of statistical significance were found:

For Rostrum Width/Basal Length,  
 $p < 0.05$

For Bulla Depth/B.L.,  $p < 0.05$

For  $m^{1-3}$  Length/B.L.,  $p < 0.002$

For  $m^4$  Length/B.L.,  $p < 0.02$

Despite the similarities, in cranial proportions and in molar gradient, between *B. tropica* and *B. penicillata*, the shape and insertion of the premolars suggest that the relationship between these two is not as close as between *B. tropica* and *B. gaimardi*. (See footnote, Section 3.)

In comparisons between *B. tropica* and *B. gaimardi*, these orders of significance were found:

For Rostrum Width/B.L.,  $p < 0.02$

For Interorbital Width/B.L.,  
 $p < 0.02$

For  $m^4$  Length/B.L.,  $p < 0.02$

For  $p^4$  Length/B.L.,  $p < 0.002$

For Bulla Length/B.L.,  $p < 0.002$

For Bulla Depth/B.L.,  $p < 0.002$

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### Abstract

A study has been made of the species of the genus *Bettongia*, which comprises *B. lesueur*, a burrowing, woolly-haired species, and *B. penicillata*, *B. gaimardi* and *B. tropica*, which three are nest-building, brush-tailed species.

*B. penicillata*, distinguished by the unique morphology of its premolars, is shown to have had a more restricted distribution than that attributed to it in current literature, and the validity of the present subspecific classification in the species is questioned.

*B. gaimardi* is shown to have had a mainland Australian distribution from south-eastern Queensland to south-western Victoria. The larger Tasmanian form, currently known as *B. cuniculus*, is considered to be conspecific with *B. gaimardi*, and is reclassified as *B. gaimardi cuniculus*.

A hitherto unrecognized species of brush-tailed bettong, native in north-eastern Queensland, is described and named *Bettongia tropica*. From *B. gaimardi*, *B. tropica* is distinguished mainly by the larger premolars and larger auditory bullae.

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